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Errors in interception can be predicted from errors in perception

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ABSTRACT

It has been hypothesised that our actions are less susceptible to visual illusions than our perceptual judgements because similar information is processed for perception and action in separate pathways. We test this hypothesis for subjects intercepting a moving object that appears to move at a different speed than its true speed due to an illusion. The object was a moving Gabor patch: a sinusoidal grating of which the luminance contrast is modulated by a two-dimensional Gaussian. We manipulated the patch's apparent speed by moving the grating relative to the Gaussian. We used separate two-interval forced choice discrimination tasks to determine how moving the grating influenced ten people's judgements of the object's position and velocity while they were fixating. Based on their perceptual judgements, and knowing that our ability to correct for errors that arise from relying on incorrect judgements are limited by a sensorimotor delay of about 100 msec, we predicted the extent to which subjects would tap *ahead of* or *behind* similar targets when trying to intercept them at the fixation location. The predicted errors closely matched the actual errors that subjects made when trying to intercept the targets. This finding does not support the two visual streams hypothesis. The results are consistent with the idea that the extent to which an illusion influences an action tells us something about the extent to which the action relies on the percept in question.

1. Introduction

Two visual pathways have been identified in the human brain: a ventral stream that connects the primary visual cortex with the inferior temporal cortex, and a dorsal stream that connects the primary visual cortex with the posterior parietal cortex. It was originally proposed that these streams process complementary attributes corresponding to the processing of the 'what' and 'where' of an object (Ungerleider & Mishkin, 1982). Goodale and Milner (1992) subsequently suggested that the two pathways process the same attributes, but for different functions. They suggested that the ventral stream deals with perceptual judgements about objects ('what') while the dorsal stream is responsible for the use of visual information about the same attributes of the objects in action ('how'): the two visual streams hypothesis.

The two visual streams hypothesis was mainly based on two types of clinical cases (Goodale & Milner, 1992, 2004; Milner

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& Goodale, 1993, 1995, 2006, 2008; Goodale, Milner, Jakobson, & Carey, 1991, 1994; but see Hesse, Ball, & Schenk, 2012; Himmelbach, Boehme, & Karnath, 2012; Pisella, Binkofski, Lasek, Toni, & Rossetti, 2006; and Schenck, 2006 for different interpretations of the clinical evidence). Patients with visual form agnosia could not adequately report objects' orientations or dimensions due to a dysfunctional ventral pathway, but could successfully interact with those same objects (James, Culham, Humphrey, Milner, & Goodale, 2003; Milner et al., 1991). On the other hand, patients with optic ataxia were unable to successfully interact with objects due to a dysfunctional dorsal pathway, but could make perceptual judgements about the objects (Milner & Dijkerman, 2001; Milner, Dijkerman, McIntosh, Rossetti, & Pisella, 2003; Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999; Perenin & Vighetto, 1988). Does this mean that information is processed separately for perceptual judgements and to guide our actions?

One distinction between processing information for perception and action is that actions often need instantaneous information, such as an object's position relative to oneself. Such information is not a characteristic of the object. It depends on one's own position. Consequently, the information changes as one moves, sometimes making it more important to get the information fast than for it to be very precise. These characteristics match the properties of the dorsal stream. Conversely, information that is very important for making judgements about an object, such as recognizing whether the object is yours, is constant over time, but relies on a detailed analysis, corresponding to the properties of the ventral stream. This distinction has led to the two visual streams hypothesis, according to which the dorsal and the ventral streams process similar information in different ways: for guiding our actions and for making perceptual judgements, respectively (Goodale & Milner, 1992). According to this hypothesis our actions are immune to many illusions because they do not benefit from many of the contextual effects that improve our perceptual judgements. Following this reasoning, visual illusions have been used to try to show this functional distinction between the two visual streams.

An alternative interpretation of these studies arises if one assumes that the involvement of each of the two visual streams is determined by the visual attribute that is used rather than by whether the task being performed is an action or a perceptual judgement (Smeets, Brenner, de Grave, & Cuijpers, 2002). Some attributes (such as egocentric position) are very rarely used in perceptual tasks, whereas others (such as colour) are seldom used to control action. Two object attributes that could be very relevant for actions as well as for perceptual judgements are an object's size and the speed at which it is moving.

The most extensively studied example of using illusions to evaluate whether there is a functional distinction between the two visual streams is the study of the influence of size illusions on grasping. There is ample evidence in favour of the idea that size illusions do not influence grasping (Aglioti, DeSouza, & Goodale, 1995; Glover, 2004; Glover & Dixon, 2002; Haffenden & Goodale, 1998). However, there is also quite a lot of evidence against this idea (Biegstraaten, de Grave, Brenner, & Smeets, 2007; Franz, Gegenfurtner, Bülthoff, & Fahle, 2000; Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; de Grave, Biegstraaten, Smeets, & Brenner, 2005; Kopiske, Bruno, Hesse, Schenk, & Franz, 2016; Mon-Williams, Tresilian, Coppard, & Carson, 2001; for reviews see; Bruno & Franz, 2009; Franz & Gegenfurtner, 2008; Schenck, Franz, & Bruno, 2011; Smeets et al., 2002; Smeets & Brenner, 2006). There are even discrepancies within single studies: an illusion that influenced the judged size of an object was found not to influence the maximal grip aperture when grasping it, but to influence how subjects lifted the object (Brenner & Smeets, 1996; Jackson & Shaw, 2000). Such discrepancies are consistent with judgements about different attributes contributing to different aspects of the action, and being influenced differently by the illusion in question. For example, the above-mentioned discrepancies within single grasping studies are consistent with judgements of size being used to determine the force needed to lift the object, but not being involved in guiding the digits to suitable positions on the object (and thereby indirectly in determining the maximal grip aperture; Smeets & Brenner, 1999). Although the studies mentioned above are all concerned with grasping movements, visual illusions have also been shown to influence various aspects of other actions, such as the amplitude of saccadic eye movements (de Brouwer, Brenner, Medendorp & Smeets, 2014; de Brouwer, Brenner & Smeets, 2016; de Brouwer, Smeets, Gutteling, Toni & Medendorp, 2015; Bruno, Knox, & de Grave, 2010; de Grave, Smeets, & Brenner, 2006), the extent of manual tracking (López-Moliner, Smeets, & Brenner, 2003), the length of pointing movements (de Grave, Brenner, & Smeets, 2004) and the speed of interception (Smeets & Brenner, 1995).

If the reason for the apparent dissociation between how illusions affect perception and how they affect action is that one is comparing a perceptual judgement of an attribute that is not used to guide the parameter of the action (judgements of size rather than of positions when comparing with the peak grip aperture in grasping; Smeets & Brenner, 1999, 2002), we would expect to see no such dissociation if the action does depend on the judgement that it is compared with. This is consistent with size illusions affecting forces (but not grip aperture) during lifting (Brenner & Smeets, 1996; Jackson & Shaw, 2000) and with velocity illusions affecting the speed (but not movement direction) of interception (Smeets & Brenner, 1995). In the present study, we will further investigate the effect of illusions on interception, and try to find an interception task in which illusions make people miss the target.

Quite specific predictions have been made as to how judgements of a target object's position and velocity determine the errors that people make when trying to tap on them (Brenner & Smeets, 2015b), so we decided to test whether an illusion that is known to influence the judged position and velocity of an object would influence interception in the manner predicted by its influence on these perceptual judgements. Previous studies have demonstrated that a speed illusion (Duncker illusion) influences the speed of the hand during interception, without a corresponding influence on interception errors (Brenner & Smeets, 1994, 2015a; Brouwer, Brenner, & Smeets, 2002; Smeets and Brenner, 1995). This lack of effect was attributed to subjects being allowed to pursue the target with their eyes (de la Malla, Smeets, & Brenner, under review). When doing so they could use information about the orientation of the eyes to guide the hand. In the present study, we test whether the position at which subjects intercept targets is biased by perceptual illusions if subjects have to intercept a target at the location that they are fixating. For this purpose, we need an illusion that affects attributes that are used in interception. Position and motion are such attributes.

It is well known that motion within a static target can make the target appear to be shifted in the direction of the motion (Arnold, Thompson, & Johnston, 2007; Chung, Patel, Bedell, & Yilmaz, 2007; Durant & Johnston, 2004; Fu, Shen, Gao, & Dan, 2004; Linares & Holcombe, 2008; Mussap & Prins, 2002; Ramachandran & Anstis, 1990; de Valois & de Valois, 1991) and that motion within a moving target changes the way in which the target appears to move (Hall et al., 2016; Lisi & Cavanagh, 2015; Scott-Samuel, Baddeley, Palmer, & Cuthill, 2011; Zhang, Yeh, & de Valois, 1993). Perceived motion is determined by a complex interaction between local and global motion signals, that is not directly predictable from the physiological responses of individual MT neurons (Hedges et al., 2011), so the embedded motion is unlikely to influence perception and action in the same way just because the effects occur before the separation into dorsal and ventral pathways (Dyde & Milner, 2002).

In the present study subjects had to perform two perceptual tasks and one action task while fixating. In the perceptual tasks they either had to judge which of two moving Gabor patches was moving faster, or which disappeared further to the right. In the action task they had to intercept the same Gabor patches at the fixation position by tapping on them. In all cases we compared Gabor patches in which the sinusoidal grating did not move with respect to the Gaussian, so that the target moved as a whole, with Gabor patches in which the grating drifted within the Gaussian, either in the same or in the opposite direction than the direction in which the Gaussian was moving.

A critical issue for quantitatively comparing the effects on perceptual judgements with those on interception is to estimate the perceptual judgements at the moment that determines the tapping error. In the perceptual tasks, targets moved in the same way as when they were to be intercepted, but the reference target disappeared 100 msec before it reached the fixation position. We chose 100 msec because this is about the time that it takes to adjust one's movements on the basis of visual information about the target's position (Brenner & Smeets, 1997), and therefore the time during which errors based on misjudging the target's position and velocity will remain uncorrected (Brenner & Smeets, 2015b). We combined the errors in the perceived velocity and the perceived position to predict the errors when tapping on the targets. We show that the errors that subjects made in trying to intercept the targets matched this prediction, indicating that there is no clear dissociation between perception and action.

2. Methods

2.1. Subjects

One author and nine naïve subjects took part in the three tasks of the experiment in three separate sessions. All subjects (age–range 25–34) reported being right handed and having normal or corrected-to-normal vision. None had evident motor abnormalities. All subjects gave written informed consent. The study was part of a program that was approved by the local ethical committee.

2.2. Apparatus

The experiments were conducted in a normally illuminated room. Subjects stood in front of a large screen (Techplex 150, acrylic rear projection screen, width: 1.25 m, height: 1.00 m; tilted backwards by 30° to make tapping more comfortable) onto which the stimuli were back-projected (InFocus DepthQ Stereoscopic Projector; resolution 800 by 600 pixels; screen refresh rate: 120 Hz). Subjects were not restrained in any way in any task. For the interception task, an infrared camera (Optotrak 3020, Northern Digital) that was positioned at about shoulder height to the left of the screen measured the position of two infrared light-emitting diodes at 500 Hz. The first diode was attached to the nail of the subjects' right index finger. Its position was the main variable of interest. The second diode was attached to the left edge of the screen (facing the Optotrak camera) and was only used to synchronize the timing of the display with that of the Optotrak. The second diode was briefly inactivated when a flash of light fell on a sensor that was placed in the path of the light directed towards the top left corner of the screen. Flashes were presented for one frame when the targets appeared. In this way, we were able to determine the position of the finger with respect to the moving target on the screen with a resolution of 2 msec (for further details see Brenner & Smeets, 2015a). Before starting the interception task, the position of the marker on the fingertip was measured when the fingertip was at four successively indicated positions on the screen. Subjects had to move their finger to the indicated position and keep it static (displacement of less than .5 mm in 300 msec). This simple four-point calibration was used to relate the position of the fingertip to the projected images, automatically correcting for the fact that the marker was attached to the nail rather than to the tip of the finger.

2.3. Stimulus and procedure

For all three tasks the stimuli were Gabor patches that consisted of a vertical sine wave grating (carrier with a spatial frequency of .29 cycle/cm) of which the contrast was determined by a Gaussian (2D envelope with a standard deviation of 2 cm in both directions) displayed against a uniform grey background. The Gabor patches (i.e., the Gaussian) always moved at a constant velocity (40 or 50 cm/sec) from the left to the right of the screen, 10 cm above the screen centre. The grating within the patches (carrier) was either static with respect to the Gaussian, so that the patch moved without changing its appearance, or else the grating drifted with respect to the Gaussian, either in the same direction as (10 cm/sec) or in the opposite direction than the Gaussian (−10 cm/sec). In all tasks subjects had to fixate their gaze on a blue 1.5 cm diameter dot located 16 cm to the right and 10 cm above the centre of the screen. We used sequential two-alternative forced-choice discrimination tasks to determine the perceived position and velocity of the patches with embedded motion. To measure errors in action we determined how subjects intercepted patches with and without embedded motion. The order of the three tasks was chosen at random for each subject.

2.3.1. *Velocity perception task*

In the Velocity perception task subjects had to judge which of two sequentially presented patches moved faster. Fig. 1A shows a schematic representation of the task. The session started with a presentation of the question that subjects had to answer during that session (Which was faster?). Every trial started with the fixation point being presented for a random period between .5 and .7 sec. After that, the first patch appeared. It moved from left to right, disappearing 100 msec before it reached the fixation point. A blank screen with the fixation point was then presented for another random period between .5 and .7 sec, after which the second patch appeared, also moving from left to right and also disappearing 100 msec before reaching the fixation point. Once the second target had disappeared subjects had to provide their response by pressing the '1' or '2' key of the computer's keyboard to indicate whether the first or second patch moved faster. As soon as they responded the next trial started. Within a trial, one of the two patches was a *standard* patch and the other was a *comparison* patch; which of the two was presented first was chosen randomly.

There were four possible standard patches: moving at either 40 or 50 cm/sec, each with embedded motion of either 10 cm/sec or −10 cm/sec. We used two target velocities that are close to each other in order to force subjects to consider visual information about the target's velocity. The comparison patches never had embedded motion. When the standard patch moved at 40 cm/sec, the comparison patches could move at either 10, 20, 30, 40, 50, 60 or 70 cm/sec, and both patches were presented for 700 msec. When the standard patch moved at 50 cm/sec, the comparison patches could move at either 20, 30, 40, 50, 60, 70 or 80 cm/sec, and both patches were presented for 540 msec. The starting positions of the patches were chosen in such a way that all of them disappeared 100 msec before they would have reached the fixation point. Each combination of the 4 standard patches and 7 comparison patches was repeated 20 times, so there was a total of 560 trials that were presented in a completely random order. A session took about 50 min to complete. Subjects could stop to have a break at any time during the session by delaying when they pressed a keyboard key to indicate their response.

2.3.2. *Position perception task*

In the Position perception task subjects had to judge which of two sequentially presented patches disappeared further to the right. The design of the task was very similar to that of the Velocity perception task. The question presented at the beginning of the session was obviously different (here: Which finishes more to the right? see Fig. 1A). Here too, every trial started with the fixation point being presented for a random period between .5 and .7 sec, followed by a first patch moving from left to right across the screen, a blank screen with fixation point for another random period between .5 and .7 sec, and a second patch moving from left to right across the screen. As in the Velocity perception task, moving patches always disappeared before reaching the fixation point. Once the second target had disappeared subjects indicated whether the first or second patch disappeared further to the right by pressing the '1' or '2' key of the computer keyboard. Again, the response initiated the next trial, with the standard and comparison patches presented in random order.

As in the Velocity perception task, there were four possible standard patches that moved at either 40 or 50 cm/sec with embedded motion of either 10 cm/sec or −10 cm/sec. Patches that moved at 40 cm/sec moved for 700 msec and patches that moved at 50 cm/sec moved for 540 msec. In both cases the patch disappeared 100 msec before it would have reached the fixation point. Comparison patches never had embedded motion. The comparison patches moved at the same velocity as the standard ones (40 or 50 cm/sec). The comparison patches either disappeared at the same position as the standard one, or 1, 2 or 3 cm further to the left or to the right. Each

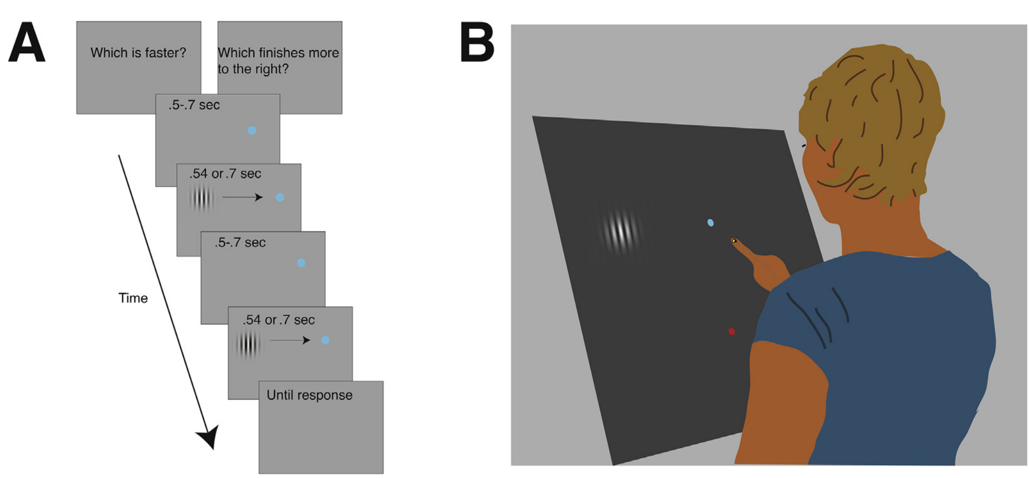

Fig. 1 — Schematic representation of the three tasks. In all tasks, subjects fixated a blue dot. (A) In the two perceptual tasks subjects had to judge which of the two sequentially presented Gabor patches moved faster (Velocity task) or disappeared further to the right (Position task). They did so by pressing a key on a keyboard. (B) In the interception task subjects started with their hand on the starting position (red dot) and had to tap the patch when it was at the fixation position (blue dot).

combination of the 4 standard patches and 7 comparison patches was repeated 20 times, so there was a total of 560 trials that were presented in a completely random order. It took about 50 min to complete the task. Subjects could stop to have a break at any time during the session by delaying when they pressed a keyboard key to indicate their response.

2.3.3. *Interception task*

In the interception task subjects had to start each trial by placing their index finger at the starting point: a 1.5 cm diameter red disk that was 20 cm below the fixation dot. Between 500 and 800 msec after the finger was placed at the starting point, the same fixation dot that we used in the perceptual task was shown and a patch appeared moving from left to right across the screen. Subjects had to try to intercept the patch by tapping on it when it was at the fixation position. Fig. 1B shows a schematic representation of the task. A tap was detected when the deceleration of the finger's movement orthogonal to the screen was more than 50 m/sec^2 while the finger was less than 5 mm above the screen and within 10 cm of the patch's path. Subjects could rest between trials at any time during the session by not placing their finger at the starting point.

The patches used in this task were the same four as the standard patches used in the perceptual tasks (patches moving at 40 or 50 cm/sec with embedded motion of 10 or −10 cm/sec), supplemented with patches with no embedded motion. The patches with no embedded motion were used as a baseline in order to account for any bias in hitting the targets that was not related to the embedded motion. Thus, in this task there were 6 kinds of patches that subjects had to intercept: patches moving at either 40 or at 50 cm/sec with embedded motion of 10, 0 or −10 cm/sec. The patches' starting positions were chosen so that the centre of the patch would reach the centre of the fixation point after 800 msec when the patches moved at 40 cm/sec and after 640 msec when they moved at 50 cm/sec (corresponding to the perceptual tasks in which the patch disappeared after 700 msec and 540 msec, 100 msec before reaching the fixation point). Subjects received immediate feedback after each tap. If subjects tapped less than 1.5 cm from the centre of the patch, it stopped moving. If the tap was also within the fixation point, a sound indicated that the trial was successful. If the tap was further from the centre of the patch, the patch deflected away from the finger at 1 m/sec for 500 msec.

There were 20 trials for each combination of velocity and embedded motion, giving a total of 120 trials. The trials were presented in random order. It took about 12 min to complete this task.

2.4. *Data analysis*

All analyses were performed with R Statistical Software (R Development Core Team, 2014). To analyse the perceptual tasks we used the *quickpsy* package (Linares & López-Moliner, 2016). For each subject we fit cumulative Gaussian distributions to the proportion of trials in which the different comparison patches were judged to be faster or to disappear further to the right than the standard patch. In doing so, we assumed that there were no ‘lapses’ in the judgements (Wichmann & Hill, 2001). The means of the underlying Gaussian distributions provide estimates of the points of subjective equality (PSE). These estimates tell us how embedded motion influences the perceived velocity and position, allowing us to predict how the illusion will affect the interception task (see below). We obtained 95% confidence intervals for each PSE by bootstrapping the data 1000 times (Efron & Tibshirani, 1994).

We determined the tapping error for each trial: the horizontal distance between the position at which subjects tapped the screen and the position of the centre of the patch at the moment of the tap. Trials in which the error was more than three times the standard deviation away from the mean for each subject, velocity and direction of the embedded motion were removed from the analysis, to be sure to remove any trials in which the subject was not trying to tap on the target or in which the tap was not detected correctly (15 trials were removed in total, 1.25% of the trials). Systematic tapping errors were obtained by averaging across trials. Confidence intervals of the tapping errors were calculated from the standard deviations per subject for each combination of target velocity and embedded motion.

In order to compensate for biases in when one hits targets that have nothing to do with the embedded motion (Brenner, Canal-Bruland, & van Beers, 2013; de la Malla, López-Moliner, & Brenner, 2014, 2012), we judged the effect of the illusion by determining the difference between the position at which subjects tried to intercept patches with embedded motion and the position at which they tried to intercept patches with no embedded motion (for the same target velocity). We combined the 95% confidence intervals of each type of patch with embedded motion and of the patch moving at the same velocity without embedded motion to obtain an estimate of the confidence interval for the influence of the illusion on the tapping error. We did that assuming that the measured errors were independent and from symmetric normal distributions.

In order to see whether the perceptual judgements can be used to predict the influence of the illusion on the action directed towards the patches, we considered a simple model to predict the error (a simplified version of equation (1) in; Brenner & Smeets, 2015b):

$$error_{predicted} = error_{position} + delay * error_{velocity} \tag{1}$$

in which $error_{predicted}$ is the predicted influence of the illusion (in cm) for the interception task, $error_{position}$ is the influence of the illusion on the judged position of the patch as determined from the PSE of the relevant standard patch in the perceptual position task (in cm), and $error_{velocity}$ is the influence of the illusion on the judged velocity of the patch as determined from the PSE of the relevant standard patch in the perceptual velocity task (in cm/sec). We use a value of .1 sec for the delay, because it takes about 100 msec to correct an on-going movement on the basis of new visual information, so we predict that the perceived position and velocity 100 msec before the tap determine the error that is made.

We determined the 95% confidence intervals for the predicted effect on interception from the bootstrapped 95% confidence intervals of the illusion effects on position and velocity judgements through standard error propagation, again assuming that the effects are independent and from symmetric normal distributions.

After calculating the predictions and determining the actual errors for each subject, velocity of the standard patch, and direction of the embedded motion, we averaged both the predictions and the actual errors across the two velocities of the patch for each subject. We then averaged the magnitudes of the effects for the two directions of embedded motion for each subject and examined whether there was a positive (Pearson's) correlation coefficient between the predicted and the actual interception errors across subjects.

3. Results

Fig. 2 shows the results for two representative subjects. For both subjects, embedded motion might have influenced the perceived position in the anticipated direction by a very small amount (Fig. 2A). For nine of the ten subjects the mean effect was in the anticipated direction. Averaged across patch velocities, the median influence of embedded motion in the Position task was .23 and −.22 cm for 10 and −10 cm/sec of embedded motion, respectively. Thus, we expect errors of about .2 cm due to the effect of the embedded motion on the judged position.

Embedded motion clearly influenced the perceived velocity (Fig. 2B). For all ten subjects the mean effect was in the anticipated direction. Averaged across patch velocities, the median influence of embedded motion in the Velocity task was 12.2 cm/sec and −9.7 cm/sec for 10 and -10 cm/sec of embedded motion, respectively. Thus, subjects seem to actually have been judging the velocity of the grating, rather than that of the patch. Based on the velocity judgements we expect an error of about 1.1 cm due to the effect of the embedded motion on the judged velocity (11 cm/sec × .1 sec; see Equation (1)).

Embedded motion clearly influenced the tapping errors (solid bars Fig. 2C). For all ten subjects the mean effects were in the anticipated direction. Their mean tapping errors were 1.19 cm and −1.48 cm for 10 and −10 cm/sec of embedded motion, respectively. The influence on the tapping errors was consistent with the perceptual effects: when the embedded motion was in the direction in which the patch was moving (blue dots and bars), the patch appeared to be closer to the fixation point (Fig. 2A) and to move faster (Fig. 2B) than it really was, both of which indicate (according to Equation (1)) that the subject will tap ahead of the target (positive values in Fig. 2C). The converse is true for embedded motion in the opposite direction. The magnitude of the errors (solid bars) is similar to what one might predict from the perceptual errors (outlined bars in Fig. 2C).

The similarity between the predicted systematic interception error and the actual systematic interception error is not only evident for the mean values and for the subjects whose data are shown in Fig. 2. Fig. 3 shows the predicted and the

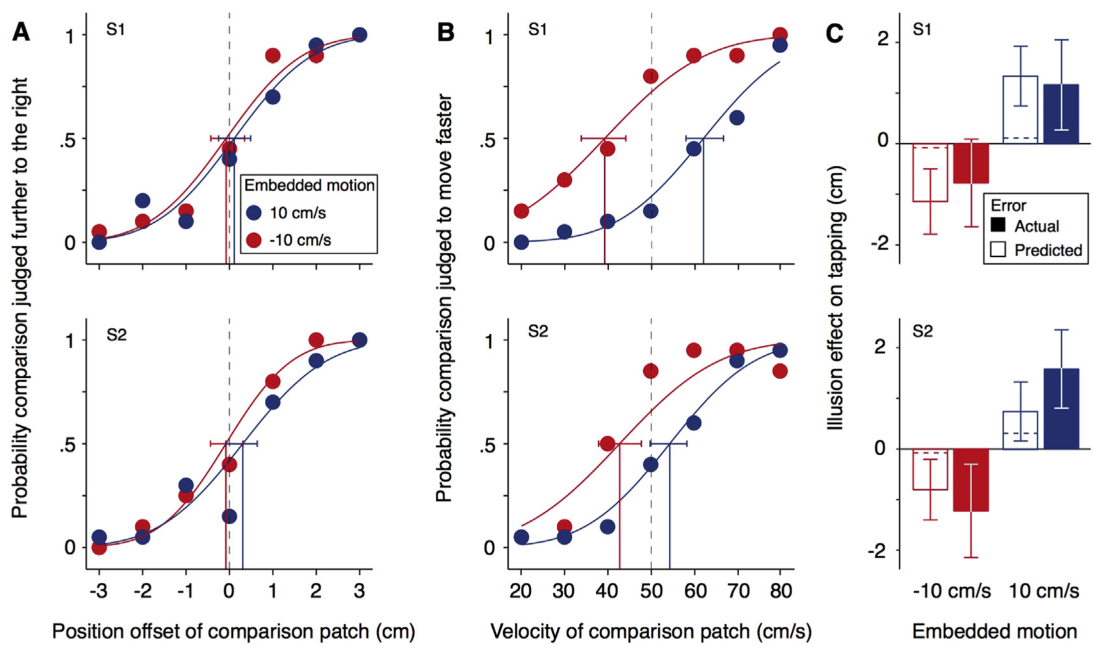

Fig. 2 – Illusion effects for two typical subjects (S1 and S2) for patches moving at 50 cm/sec with embedded motion in the opposite (−10 cm/sec, red) or same (10 cm/sec, blue) direction as the motion of the patch itself. (A) Position perception task; (B) Velocity perception task. Dots indicate the fraction of trials on which the comparison was judged to disappear further to the right or to move faster than the standard patch. Psychometric functions (curves) were fit to the perceptual judgements. The coloured vertical lines indicate the PSE and the coloured horizontal error bars indicate the 95% confidence interval of the PSE. The grey dashed vertical lines indicate no effect of the illusion. (C) Interception task. Solid bars indicate differences in tapping errors between patches with and without embedded motion. Outlined bars indicate the expected differences given the results of the perceptual tasks, with the horizontal dashed lines separating the (small) contribution of misjudging the position from the (large) contribution of misjudging velocity. Positive values indicate tapping ahead of the target. Error bars are 95% confidence intervals.

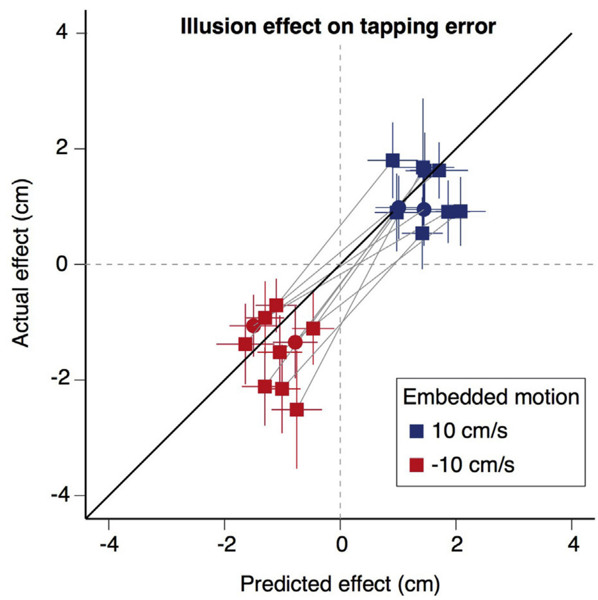

Fig. 3 – Measured influence of the illusion on tapping errors in the interception task as a function of the effect that one would predict on the basis of the two perceptual tasks. A set of two symbols connected by a grey line represents an individual subject's values for the two directions of embedded motion (indicated by the colour), averaged across the two velocities of the (standard) patch. The disks represent the results for the subjects S1 and S2 whose data are shown in more detail in Fig. 2; the squares represent those for the other subjects. Error bars are 95% confidence intervals. The dashed lines indicate no influence; the black line is the unity line, indicating a perfect match between the predicted and the actual effect.

actual effects of embedded motion for all ten subjects. The actual effects are close to the ones one would expect given the misperception of these patches' positions and velocities: the dots fall close to the unity line. For most of the points, the unity line is within the 95% confidence limits. Thus, the way in which the embedded motion influenced performance in the interception task was also to a large extent quantitatively consistent with the effects that were found in the perception tasks. However, there was no positive correlation between the individual average magnitudes of the predicted and actual effects (across subjects).

4. Discussion

Our results clearly show that embedded motion has a strong influence on how fast a patch is seen to move, complementing similar findings for the influence of embedded motion on the *direction* in which a patch appears to move (Lisi & Cavanagh, 2015; Zhang et al., 1993). We also found a small influence of embedded motion on the perceived position of the patch, in accordance with previous reports (Arnold et al., 2007; Chung et al., 2007; Kerzel & Gegenfurtner, 2005; Linares & Holcombe, 2008; de Valois & de Valois, 1991). Most importantly, we show that the way in which embedded motion causes the patches' positions and velocities to be misperceived can explain the effect that embedded motion has on where subjects tap when trying to intercept them (Fig. 3). Subjects tapped ahead of the targets when the embedded motion was in the same direction as the envelope's motion. Such embedded motion makes the patch appear to be moving faster and perhaps to be slightly closer. Tapping ahead of such targets is the error one would expect, because if the targets were really nearer and moving faster, one would need to hit earlier (blue symbols in Figs. 2 and 3). The opposite effect is expected and found when the embedded motion is in the opposite direction than the envelope, making the patches appear to move more slowly and perhaps to be slightly further away (red symbols in Figs. 2 and 3).

In this study, we not only demonstrate that people make errors in action that are in the same direction as the ones one would expect given the misperception of the moving target's position and velocity, but we use a simple model (Equation (1)) to combine the perceptual effects in order to quantitatively predict the errors that we expect to find when trying to intercept the target. This prediction matched the subjects' actual errors quite well (Fig. 3). Nevertheless, there are some subjects for whom the deviation from the prediction is slightly larger than expected (points further away from the unity line than one would expect considering the 95% confidence intervals; Fig. 3).

A possible reason for *individual* errors deviating from the predictions is that we consider a fixed visuo-motor delay of 100 msec when calculating the predictions (based on approximate average response latencies in previous studies; Brenner & Smeets, 1997; 2015b). The average results are consistent with an average latency of 100 msec, but when looking at individual subjects' data it might have been better to consider that the visuo-motor delay might differ between subjects. A 10 msec larger value for the visuo-motor delay would lead to a 10 percent larger predicted effect for the error in judging the velocity. Not considering such between-subject variability when calculating the predicted error (Equation (1)) might contribute to the somewhat larger discrepancies between the predicted and actual errors in Fig. 3 for some subjects. A second factor that we did not take into account in our predictions is that in interception, subjects not only use the velocity of the present target, but are also influenced by expectations based on previous trials (de Lussanet, Smeets, & Brenner, 2001). It is very likely that this reliance on previous trials will have differed between subjects. Another factor that we do not consider and that might differ across subjects is the extent to which they maintained perfect fixation in all the tasks. Not taking differences in visuo-motor delays and in eye movements between subjects into account might explain why we did not find a correlation between predicted and actual errors across subjects.

4.1. *Misperceiving the position and the velocity*

Illusory motion-induced shifts in the position of a Gabor patch have been reported in numerous studies. In such studies, the position of a stationary Gaussian window was misperceived in the direction of the motion of the carrier grating (Bressler & Whitney, 2006; Chung et al., 2007; Fu et al., 2004; Linares & Holcombe, 2008; Ramachandran & Anstis, 1990; de Valois &

de Valois, 1991). This illusory motion-induced shift in position has been shown to depend on factors such as contrast (Arnold et al., 2007), duration of presentation (Arnold et al., 2007; Chung et al., 2007), carrier characteristics (Arnold et al., 2007; Chung et al., 2007), delay between when the stimulus is seen and when the judgement is made (Yamagishi, Anderson, & Ashida, 2001) and the task that is used to measure it (Kerzel & Gegenfurtner, 2005; Yamagishi et al., 2001), so we tried to match as many details as possible between the perceptual and action tasks in our study. Considering how well we could predict the tapping errors, the task-related dependencies cannot have been very large.

The influence that we found for the position task (.2 cm, corresponding with about .2°) is within the range of values reported in previous studies using various methods (.03° to .4°; de Valois & de Valois, 1991; Kerzel & Gegenfurtner, 2005; Chung et al., 2007; Arnold et al., 2007; Linares & Holcombe, 2008). As far as we know, this is the first study that measures the misperception of both the *position* and the *velocity* of a stimulus that contains embedded motion. It is clear that if our predictions for how these perceptual errors contribute to interception errors (as expressed in Equation (1)) are correct, embedded motion will have a much weaker influence on interception through its effect on the perceived position of the patch (on average .2 cm) than through its effect on the perceived velocity (on average 1.1 cm). We want to point out that although the influence on the judged position might be negligible, it must be considered, both because it is a component of the theoretical basis for the prediction, and because even if removing the influence of misjudging the position would hardly influence the match between the actual and predicted effects, not considering the judged position would influence the confidence intervals of the predictions.

4.2. A comparison with misperceiving the direction of a Gabor patch's movement

Gabor patches have been used before to study the presumed dissociation between perception and action (Lisi & Cavanagh, 2015). When the carrier of a Gabor patch moves in the orthogonal direction to the motion of the envelope, rather than in the same or opposite direction as in the present study, the patch appears to be moving in a different direction than its true direction of motion. Lisi and Cavanagh (2015) suggested that for such patches the influence of the carrier's motion on saccades towards the patch is inconsistent with the perceived motion of the patch. Morgan (2015) has already pointed out that Lisi and Cavanagh may not have managed to make the perceptual and action tasks precisely comparable. In the present study, our strategy for avoiding this problem was to predict the errors that would be made when intercepting a target by tapping on it by combining what we know about how this action is guided by visual information (Equation (1)) with the influences that embedded motion has on the perceived position and on the perceived velocity. Although Lisi and Cavanagh's experiments involved moving the eyes rather than the arm, they are similar to ours in that they also require one to predict the future position of a moving target. In both cases one can expect systematic errors to arise from using the misjudged motion to make such prediction. In their study, the motion of the carrier influenced the apparent *direction* of the patch's motion, whereas in the present study it influenced the patch's apparent *speed*. In both cases, we might also find a small effect of misjudging the position. We will therefore consider their findings in the same manner as ours, and show that they are consistent with our conclusion.

In our study, we considered a visuo-motor delay of 100 msec. In Lisi and Cavanagh's study, the equivalent delay is presumably the time between when the definitive goal position for the saccade is determined and the end of the saccade. Although this delay might be shorter than 100 msec, it too should be an approximately constant value. So, what errors would we expect with such a constant delay when misjudging the direction of motion? Assuming that people hardly misjudged the position, as in our study, and considering that their targets moved at a constant speed with constant embedded motion, the *error* in judging the target's future position due to misjudging the direction of motion should be more or less constant. Consequently, the landing positions of saccades towards the target should follow the true motion trajectory, but with an offset in the direction of the carrier motion. The data that Lisi and Cavanagh show are qualitatively consistent with this expectation. Their Figures 1E and 1F show that the landing points follow the true positions, and the reported significant difference between saccade landing positions for targets at the same position with opposite carrier motion show that there is some influence of the carrier motion. So their data are consistent with our conclusion. The inconsistency is at another level (Smeets, Sousa, & Brenner, 2009): embedding motion in the orthogonal direction to a patch's motion can influence the patch's apparent direction of motion in a manner that is inconsistent with its apparent displacement, as is illustrated in the Supplementary Material.

4.3. Where to go now with the what and how pathway

According to the most widely advocated version of the two visual streams hypothesis, whereby action is guided by a dorsal visual stream that only processes accurate metric information, while perception relies on a ventral visual stream that also processes other sorts of information, misperceiving moving patches' motion as a result of embedded motion should not influence actions directed towards the patches, because according to that hypothesis illusions should not influence actions. Misperceiving the moving patches' motion clearly did influence such actions. Is this finding enough reason to reject the two visual systems hypothesis altogether?

The strongest support for the two visual streams hypothesis is that patients with a damaged ventral pathway are impaired when making perceptual judgements about objects, but not when directing their actions towards the same objects, whereas patients with a damaged dorsal pathway can make adequate perceptual judgements about objects, but cannot direct appropriate actions towards the same objects (Goodale & Milner, 1992, 2004; Milner & Dijkerman, 2001; Milner et al., 2003, 1999; Perenin & Vighetto, 1988). This is often interpreted as evidence that information for perception and information for action are processed independently of each other. Findings that suggest that illusions influence perceptual judgements more than they influence actions (Aglioti et al., 1995; Glover & Dixon, 2002; Haffenden & Goodale, 1998; Haffenden, Schiff, & Goodale, 2001) are often interpreted as showing that the two streams process attributes in different ways. In fact, any difference between measured effects on perceptual tasks and on action tasks is readily considered as support for the two visual streams hypothesis.

In our study, the carrier motion influenced action in accordance with its influence on perception. This does not support the idea that similar information is processed separately and differently for perception and action, as proposed by the two visual streams hypothesis. It is consistent with a distinction between a dorsal stream that analyses attributes such as position or velocity that are most relevant for our actions ('where') and that is closely connected to areas that guide our actions, and a ventral stream that analyses attributes that are most relevant for recognizing objects and situations ('what') and that is less directly connected to the areas that guide our actions (Ungerleider & Mishkin, 1982). If one accepts this description of the distinction, that can explain the patients' specific deficits but does not involve processing the same attributes separately in different ways for perception and action, it makes sense for an illusion that influences instantaneous perceptual judgements of an object's position and motion, attributes that are directly relevant for interception, to influence how we intercept an object.

Thus, we contend that there is no fundamental distinction between the analysis of visual information for perception and for action. In fact, looking carefully at what is processed in the dorsal pathway might help determine how our movements are controlled. Not that ventral processing cannot influence actions, there is a reasonable consensus that information processed in the ventral stream can influence actions; it is just not the preferred route (Faillenot, Toni, Decety, Gregoire, & Jeannerod, 1997; Hoeren et al., 2014) and it often takes more time for such information to do so (Veerman, Brenner, & Smeets, 2008). Thus, we would like to argue that finding dissociations between perception and action simply indicates that one is comparing the wrong tasks. If grip aperture is influenced differently than size judgements, the grip aperture is probably not determined by estimates of size (Brenner & Smeets, 1996; Smeets & Brenner, 1999). Accepting this leads to exciting new ways of determining what information is used to guide specific actions. Following such reasoning, the findings reported here support the idea that interception is guided by the target's judged position and velocity, with constant corrections being made until about 100 msec before the tap (Brenner & Smeets, 2015b).

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Supplementary data

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